



## Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

THE  
BOTANICAL GAZETTE

FEBRUARY 1911

THE ANATOMY OF THE SPORELING OF MARATTIA  
ALATA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 142

GRACE MIRIAM CHARLES

(WITH PLATES IX-XII AND THREE FIGURES)

The Marattiaceae combine to a unique degree the interest of an extremely ancient family with the significance of connections not only with other fern families but with the origin of seed plants. The recent discovery of the latter connection calls for more knowledge of the vascular anatomy of the living Marattiaceae, based upon abundant material.

**Historical**

The first studies of the anatomy of the Marattiaceae were based upon the mature stem of *Angiopteris evecta*. As the anatomy of this genus is the most complicated in the family, the first investigators, DE VRIES and HARTING (7), in 1853, concluded that the vascular system is composed of a tangled net of bundles running in every direction through the stem; and that the strands make a spiral of several cycles, which finally run out into the leaf traces. They made no distinction between leaf traces, stem bundles, and cortical roots.

In 1864 METTENIUS (21) investigated the stem of a large plant of *Angiopteris evecta* that had been languishing for eleven years before it was used for research. He considered that the vascular tissue is arranged in a series of concentric meshed zones or funnels, whose apex is at the base of the main axis of the stem and whose obliquely running bundles pass off from the periphery as leaf traces; that these leaf traces contain a definite number of bundles from

the peripheral zone, with the addition of two strands from the second zone; and that the gap in the second zone is repaired by a strand from the third, and so on through the four or five concentric zones that compose the stele. Toward the top of the broad stem the strands united into broad bands. METTENIUS thought that this might be due to the unhealthy state of the stem he used. In 1900 Miss SHOVE (26), reinvestigating a mature stem of *A. evecta*, confirmed his theory. She found a further difference in her material in the absence of strands from the second zone in the leaf traces. Otherwise her results confirmed those of METTENIUS.

In 1877 DE BARY (6) accepted METTENIUS' description of the mature stem of *A. evecta*, but found in the young stem a typical fern cylinder. In 1889 KÜHN (17) extended the work on juvenile forms to *Kaulfussia aeschylifolia* and *Marattia fraxinea*. Their steles consisted of a cylinder of bundles surrounding a central strand, which fused with the peripheral cylinder and went out as part of a leaf trace. He supposed that the place of the central strand was taken by a peripheral bundle bending in to the center. In the older plants of *Marattia*, instead of one there were two concentric series of bundles in whose center again was a medullary strand. In *Kaulfussia* the central strand was single, in *Marattia* it was made up of different strands at different levels.

Two important contributions to the knowledge of the anatomy of the Marattiaceae were made in 1902. (1) FARMER and HILL (9) investigated the young sporeling of *A. evecta*, filling in gaps in their material with *Marattia fraxinea* and *Kaulfussia aeschylifolia*. They found in the sporeling a single solid protostele which passed by a medullated stage to dictyostely or solenostely as the gaps are repaired. They found that the skeleton of *Marattia* is simpler than that of *Angiopteris*, because the leaves are not so crowded, although the leaf gaps are larger. (2) BREBNER (3) found that the sporeling of *Danaea alata* also starts with a protostele which does not pass through a medullated stage, but becomes crescentic after the departure of a variable number of leaf traces, and passes directly into the solenostelic stage. The medullary strand arises as a branch from the interior of the solenostele.

JEFFREY (15) in 1903 examined young stems of several species

of *Danaea* and one specimen of *Marattia fraxinea*, all of which had reached the stage of an amphiphloic siphonostele with a medullary strand. He found a tendency of internal phloeoterma to degenerate, and lists the Marattiaceae with pteridophytes that have developed endarch collateral bundles. He gives no description or figures of the stele in this stage.

It is evident that there is a fundamental difference in the transition from protostele to solenostele in *Angiopteris* and *Danaea*, that there are other important points in the various accounts that do not harmonize, and that *Marattia* has been examined only incidentally from a few specimens. It seemed desirable, therefore, to make a thorough study of a large number of sporelings of *Marattia* in all stages of development.

### Material

A very generous supply of sporelings of *Marattia alata* of various ages was sent from Xalapa, Mexico, in November 1908 by Professor BARNES and Dr. LAND, who described to me the places in which the young sporelings were found. The most favorable locations were on the east slopes of the mountains near Xalapa, at an altitude of about 1140 meters, the temperature averaging about 30° C. The rainfall is 250 cm. per year, and although it is not evenly distributed, the moisture supply is sufficient to support a dense tropical rainy forest. In some places the upper vegetation had to be cut away to allow enough light to reach the ground to see the sporelings and prothallia. The most abundant supply of sporelings grew on the steep bank of a mountain torrent, in a soil composed of volcanic ash and yellow clay. Many of the youngest plants grew under the shelves made by the washing down of the surface; in one spot they grew just out of reach of the spray from a waterfall.

The prothallium may persist until the sporeling has five or six leaves, or the sporeling may become independent when its primary root is only a few millimeters long. The smallest sporeling, illustrated in fig. 4, had a primary root about 4 mm. long, and a cotyledon of the same length, whose blade was just forked. As the leaf grows older, the veins dichotomize further, and the cotyledon becomes spatulate. The first four or five leaves are of this type,

then unequal dichotomy of the middle vein sets in. Soon two lateral veinlets become prominent and form the midribs of two lateral lobes. This begins at about the 25th leaf. More pinnae are added in the same way until the pinnate adult leaf is established. The primary root is sparsely covered with coarse root hairs to within a millimeter of the tip. Hairs are less numerous on the secondary roots; and in the later roots the endophytic fungus also is less than in the primary root. The cortex of the stem, growing downward around the primary root, carries the first leaf traces down. Decay early attacks the primary root and works upward into the base of the stem. The secondary roots grow to a great length in proportion to the size of the plant, and seldom branch. In specimens 4 cm. long and 1 cm. in diameter roots extend a meter or more from the plant.

The sporelings examined ranged from the small one described to plants 2-5 cm. in diameter and 5 cm. long. Fig. 5 shows the tuberous form, the persistent swollen leaf bases (*l*) which with the stipules (*s*) hide the surface of the stem, the roots (*r*) that penetrate the old leaf bases, and the apex (*a*) inclosed by the interlocking stipules of the young leaves. The tendency to dorsiventrality shown by older *Angiopteris* stems does not appear in *Marattia*; the slight bend in a few specimens might easily be due to conditions of growth. The upper half of three of the larger plants elongated in proportion to the diameter, giving a flask-shaped contour to the plants. On the neck of the flask the leaves were separated by 0.5 cm. This change of habit from the bulky leaf-covered base was accompanied by an important simplification of the vascular anatomy that will be described later.

### Methods

Part of the plants were killed when they were gathered, in a mixture of 50 per cent alcohol and 4 per cent formalin; part were sent to Chicago in damp moss and killed in the laboratory in chromacetic acid. They were imbedded in paraffin and the small sporelings cut 10  $\mu$  thick, the large ones 15-20  $\mu$ . A week or more in the oven at 52° was necessary to infiltrate the older stems. The stain best adapted for general differentiation of

vascular tissues was found to be the safranin-anilin blue combination. Early stages in the development of mucilage ducts came out better in Delafield's hematoxylon and safranin.

A clear conception of the course of the bundles can be gained rapidly by building up a clay model molded to match section by section. Though the proportions are not exact in this free-hand method, the relation of the bundles to each other is as accurate as in the wax models, and the saving of time is enormous.

### Investigation

In the development of the stele of *Marattia alata* three stages stand out sharply: (1) the protostele; (2) the amphiphloic siphonostele, or solenostele; and (3) the polycyclic dictyostele. The transitions from one stage to the next, because they are rapid and varying, are the points about which wide differences of opinion center. Of the two transitions, that from the protostele to the solenostele is the most variable among ferns.

#### PROTOSTELE TO SOLENOSTELE

In the Schizeaceae (BOODLE 1), the Cyatheaceae, and the Polypodiaceae (GWYNNE-VAUGHAN 11), the first appearance of parenchyma in the protostele is at the periphery of the protostele at points just above the departure of leaf traces. The transformation works gradually inward. The internal parenchyma is therefore always in contact with the cortical parenchyma. In the *Lindsaya* type of stem and in *Matonia* (TANSLEY and LULHAM 27, 28) internal phloem is differentiated within the xylem and comes in contact with the peripheral phloem at the leaf gaps. In *Pteris* (LECLERC DU SABLON 19) a pith develops within the xylem.

In *Helminthostachys* (LANG 18) the xylem, though sometimes solid, usually has parenchyma often conspicuous in the center, constituting a pith. Just below the origin of the first leaf trace the pith, if present, increases in size and is continuous with the parenchyma between the xylem of the leaf trace and that of the stele. If the stele is solid in the lower part of the internode, parenchyma appears in the center of the xylem in preparation for the departure of the leaf trace.

In *Angiopteris* (FARMER and HILL 9) certain cell rows in the solid protostele cease to differentiate as tracheids, and form a pith which rapidly increases in importance, for the leaf traces soon involve the whole thickness of the xylem ring. As soon as gaps are left, the annular appearance is lost, peripheral phloem dips down and borders the pith, and then internal endodermis is differentiated as a late and secondary occurrence. In *Danaea* (BREBNER 3) what appears to be pith separates the xylem of the outgoing leaf traces from the stele, and the stem passes at once from the protostelic to the dictyostelic condition.

In *Marattia* the protostele, usually solid at the cotyledonary node, may contain parenchyma cells, as in fig. 6. This is not definitely related to the center of the stele. When the first leaf trace goes off, a bay of the peripheral parenchyma may extend across the xylem. In this bay there may be isolated xylem elements which disappear later or join one or the other of the main xylem masses. The stele may become solid above and repeat the same process in giving off 4-9 more leaf traces, or it may contain scattered parenchyma from this time on. In the latter case the line of division for the next leaf trace is marked by the largest area of inclosed parenchyma. As in *Danaea*, a combination like the simultaneous departure of two or more leaves, or of a root and leaf, may give a temporary annular appearance (fig. 7), where the root trace (*rt*) is going off opposite the leaf trace (*lt*).

The stele may return to the solid protostele above such a cylindrical stage. The first leaf traces may take off half of the elements of the protostele. Later, the stele increases in size in proportion to the leaf traces, so that the line of division between stele and leaf trace cuts in a curve instead of straight across the stele (text fig. 1). Phloem and endodermis close in behind the leaf trace over the concave as over the plane surface of the protostele (fig. 8). Soon a leaf trace goes off from the side opposite the curve before it has rounded out (fig. 9). This leaves two segments of the stele separated by parenchyma (fig. 10). The diagrams (figs. 11-21) show the start of the next leaf trace, the penetration of phloem into the stele from the opposite side (figs. 13-15), its withdrawal as the strands close together (fig. 16);

also the repetition of this process for the next leaf, when the phloem closes around the xylem strands (fig. 17) and then disappears on the side where the former leaf went off (fig. 18). At the departure of leaf 3, endodermis as well as phloem penetrates between the two xylem strands (fig. 19), and in fig. 20 the cylinder with internal phloem and endodermis is established. The transition from protostele to solenostele with leaf gaps is represented in text fig. 1.

*Angiopteris*, *Danaea*, and *Marattia* agree more closely in structure than in interpretation of the tissues concerned in this transition from protostele to solenostele. The difference in interpretation involves the question whether the tissue not xylem within the endoderm is cortical or stelar. FARMER and HILL (9) are inclined to regard only vascular tissues as stelar. This leads to the difficulty of determining what tissues are vascular and what are cortical when there is no histological differentiation. At one level they regard a tissue as xylem parenchyma which in another closely related section they call pith (9, pl. 16, figs. 10, 11). The confusion caused by setting aside as non-vascular the pith in the Marattiaceae is the greater because of the widespread tendency to lignify only part of the xylem parenchyma. The primary as well as later roots may have a solid xylem core, or may be lignified only at the poles. The cotyledonary node, usually solid, may contain scattered parenchyma, and the bundles of the dictyostele have extensive bands of parenchyma (fig. 22). Another difficulty in the way of regarding this pith as non-vascular in the Marattiaceae is that the parenchyma is rarely definitely localized in the center of the stele, so that similar stages in the development of the stele of two plants of the same species would demand as different interpretations as those given to *Angiopteris* and *Danaea*. On the other hand, the parenchyma



FIG. 1.—Diagram model of young stem in transition from protostele at the base to siphonostele at the top; the leaf traces leave constantly deeper crescents in the stele.



that appears to separate the xylem of the outgoing leaf trace from the stele cannot be lightly dismissed, for the early appearance of this tissue related to more than one leaf is probably the origin of the pith in the Marattiaceae.

The obscurity of this transition is due to the telescoping of the dictyostelic into the protostelic stage. A slight extension of this process would result in the simultaneous origin of two or three leaves at the cotyledonary node, from which a dicotyledonous habit may have been derived in some offshoot of the family.

Rarely the solenostele forms a complete cylinder. It is generally broken by two or more leaf gaps, whose large size and close arrangement cause them to overlap. At this stage the bundle arrangement is like that in the Dicksonieae, some of the Polypodiaceae, and *Ophioglossum*. The last differs from the others in the collateral structure of the bundles. In some stems of *Marattia* the tendency toward a reduction of internal phloem and endodermis, referred to by JEFFREY (15), appears. This is not uniform, however, and is more likely to appear in the medium sized than in the larger stems.

#### THE MEDULLARY SYSTEM

When the stele reaches a diameter of 2-4 mm., a medullary strand appears and initiates the final stage in the development of the stele. It may originate in three different ways: (1) Most commonly it branches from the inner surface of the solenostele. Protophloem, otherwise absent on the inner surface of the stele, appears in a patch, which is bulged outward by an increase in parenchyma (fig. 23, *pph*), and later xylem elements increase at that point. Usually a root is given off from the external surface of the bundle opposite this branch (fig. 24). This is the origin described by FARMER and HILL (9) and BREBNER (3) as a "local hypertrophy of the internal phloem." (2) It may arise by a branch which runs into the pith from the upper part of the margin of a leaf gap. (3) The pith may develop a cambium which gives rise to a strand of phloem in the center of which xylem then forms. The xylem may run 0.3 mm. before a commissure connects it with the main vascular system.

The course of the medullary system is relatively uniform in different stems. The strand runs upward through the medulla toward a leaf gap that is about to close (fig. 25). It joins one of the margins of the gap, the strand on the other margin closes in, and the three strands form a plate of vascular tissue from whose outer surface a root usually goes off (fig. 25, *rt*). The medullary strand soon frees itself again while a leaf trace goes off from the vascular plate above the point where the medullary strand joined the main vascular system. Farther on in its course the medullary strand sends a short branch into the main system, and this is not given off again but goes out with a leaf trace (fig. 25, *ms*). As the leaf traces become more crowded (text fig. 2a) the medullary strand divides into a greater number of parts, which join the main system at the closing of the leaf gaps. Occasionally a gap closes without a strand from the medullary system. At this stage *Kaulfussia* (17) and *Archangiopteris* (12) closely resemble *Marattia*.

Further complications of the medullary system of *Marattia* come from combinations of anastomoses and branching (text fig. 3). In *Matonia* the second cylinder is developed from the solid central strand



FIG. 2a.—Exterior view of diagram model of the stele at the stage when the medullary strand appears; the medullary strands can be seen through the upper leaf gap.

in the same way that the protostele in it becomes a siphonostele, by the differentiation of a strand of phloem in the center of the xylem. This repetition of the process by which the first cylinder was made does not take place in *Marattia*, but the medullary system becomes cylindrical by the anastomosis

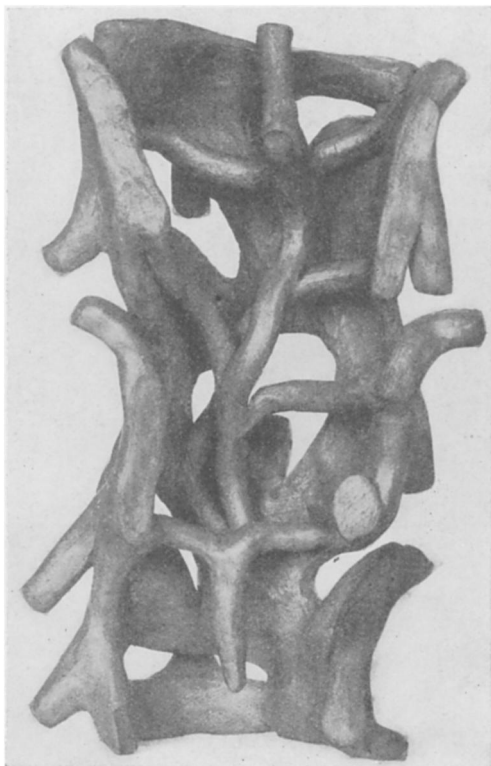


FIG. 2*b*.—The same as fig. 2*a*, with the side cut away to show the course of the medullary strand.

of two central strands (text fig. 3) in one case, although there are suggestions that the cylinder may also be formed by the branching of the strand as KÜHN (15) suggests. In the one clear case of the formation of the second cylinder in my material two medullary strands fuse to form a crescent. A branch from one horn of the crescent passes over to the other horn, then a strand from the first horn is cut off and runs out to a leaf gap. Further branching breaks up the secondary solenostele.

On account of the spiral arrangement of the leaves, the medullary strand that shares in closing a leaf gap at one level makes part of the vascular tissue of the leaf above in that rank. When the crowding of the leaves breaks the regularity of the spiral the medullary strand is less definitely related to the leaf traces. The influence of the compact form of the stem is further emphasized in the stems described above whose upper half elongates. In these the medullary strand

branches less and less frequently, until it finally joins the main vascular system and is not given off again (fig. 25). At the same time the strands of the main vascular system unite into a solenostele with a single leaf gap. This is the same sort of behavior as that in the plant examined by METTENIUS (21). The compact habit of *Marattia* is therefore responsible for two of its most striking differences from the *Psaroniae* (22): the shape of the bundles, which are band-shaped in *Psaronius* and elliptical in *Marattia*; and the relation of the medullary system to the leaf traces.

The relation of the roots to the external and to the medullary systems differs in the mature stem examined by Miss SHOVE (26) and in the young stems of *Marattia*. In the latter the main root supply joins the external system, while the medullary system has a few small roots. In *Angiopteris* the largest number of roots is attached to the internal system. This difference may be due to the greater importance

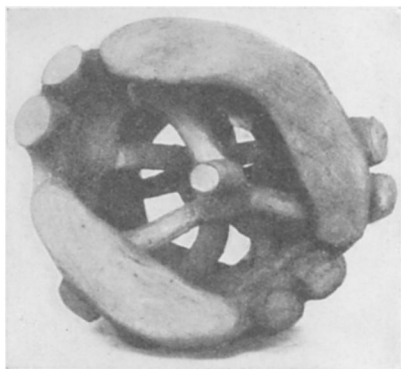


FIG. 2c.—Upper end view of fig. 2a.

of the internal system in the older stem, or to the possibility that the meshes that apparently belong to the external system in the mature stem really belong to the leaf traces, and the second zone is homologous with the main vascular system to the young stem.

In comparing the medullary systems of *Marattia* and the solenostelic ferns described by GWYNNE-VAUGHAN, some important differences appear. In the latter the origin of the system is the elaboration of a thickened leaf gap margin. The thickening works upward and downward, and in *Alsophila* (11) the strands are decurrent into the pith. In *Marattia alata* the origin is from an internal branch above a leaf gap, from the top of a leaf gap, or from a cambium in the medulla. In the solenostelic ferns the connections of the medullary with the main vascular system are generally at the nodes and along the leaf gap margin, although in *Pteris elata*

it connects at the anterior end of the leaf gap. In *M. alata* it joins the external system in the internodes, is freest at the nodes, and is concerned with the closing of the leaf gap. In the solenostelic ferns roots are not connected with the internal system as they are in the Marattiaceae. In such solenostelic ferns as have more than one concentric cylinder in the medullary system, as in *Matonia*, the

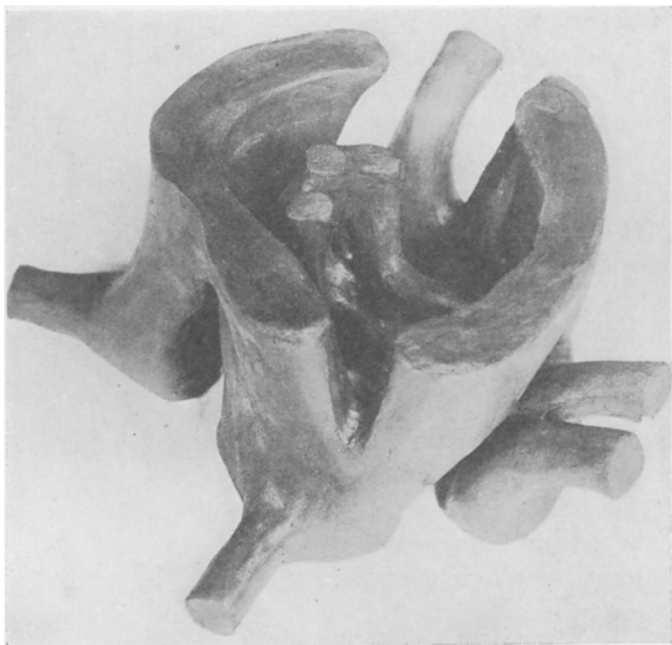


FIG. 3.—View from the upper side of a model, showing the origin of a medullary cylinder from the anastomosis and branching of two medullary strands.

formation of the second cylinder is markedly different from that in *Marattia*. In the Cyatheaceae the medullary strand takes part in the formation of several leaf traces, in *Matonia* it is a definite part of a single trace. In *Marattia* it shares in forming the region from which a leaf trace goes off.

If the medullary system of Marattiaceae is homologous with that of the Dicksonieae, Cyatheaceae, and Polypodiaceae, modifications must have taken place in the Marattiaceae. The place of

origin must have shifted upward and sidewise, so as to come above a leaf trace instead of along the margin of the gap left by it, as has taken place in *Alsophila*. The later connections must have made the same change in relative position of internal and external systems. In view of the wide distribution of medullary strands in remote groups of the pteridophytes, however, it is not certain that they are homologous even in these closely related families.

A comparison of the young stem of *Marattia* with that of *Psaronius* shows some points of resemblance more sharply than appear in the mature vascular system. The band-shaped bundles, the close relation of the medullary system to the leaf traces, and the simple leaf traces are alike in the young *Marattia* stem and in *Psaronius*. The absence of roots on the medullary system of *Psaronius* may be due to the relatively small gaps in the peripheral cylinder. The slight relation of the peripheral bundles to the leaf traces may be due, as RUDOLPH (21) has suggested, to the ranked or simple spiral arrangement of the leaves. It may be that the tendency to free origin and ending of medullary strands in *Marattia* indicates a reduction from the high state of development of such strands in *Psaronius*, as such similar free endings have been interpreted in the petioles of *Ceratozamia* (DOREY 8) and *Botrychium* (CHRYSLER 5).

#### PROTOXYLEM

The variability of protoxylem noted by GWYNNE-VAUGHAN (11) and TANSLEY (28) in Filicales generally reaches a high expression in *Marattia alata*. The first xylem elements to develop appear at the cotyledonary node. They may be the slender spiral tracheids common in ferns, similar small vessels with reticulate thickenings, as in *Dicksonia apiifolia*, or stretched scalariform vessels of the same caliber as the other elements of the xylem strand; or there may be no distinction between the first vessels and those developing later as in *Angiopteris* (FARMER and HILL 9) and *Danaea* (BREBNER 3). In the last case the change to the primary root is brought about by a reduction in the xylem at opposite sides of the bundle, development of protoxylem at the ends of the xylem band, and disappearance of phloem at the ends and increase at the sides of the xylem. In two primary roots there were three poles instead

of the two that prevail generally. As the pericycle is delicate and irregular, the protoxylem of the root often abuts on the endodermis.

In a few specimens spiral exarch protoxylem is present in the cotyledonary node. This is continuous with the protoxylem at the poles of the primary root and in the first leaf trace. In other stems the mesarch position characteristic of the older stem appears at the cotyledonary node. The same unsettled condition persists in the solenostele, although an examination of the apical region shows that the first elements lignified are toward the center of the stem. In the strands of the dictyostele definite protoxylem points appear in an endarch position, with occasionally one or two centripetal elements beyond them (fig. 22). These bundles do not show the distinction between large bundles with mesarch or no protoxylem, and small strands with endarch protoxylem observed in *Angiopteris*.

The cotyledonary trace shows the same kind of variations in the position of the protoxylem as the cotyledonary node. It may be exarch where it joins the stele (fig. 26) and gradually shift to mesarch (figs. 26-30) in the petiole; no protoxylem may be distinguishable in the trace near the stele, but a development of it in a mesarch position occurs while the trace is passing through the cortex; or the trace may consist of only two or three scattered elements. The next three or four leaves are mesarch, and may become endarch in the upper part of their course. The older leaf traces are endarch as in *Angiopteris* and *Danaea*.

#### APICAL MERISTEMS

The apical regions of *Marattia* have been the source of much difference of opinion. HOFMEISTER (13) described a single deep triangular apical cell for the Marattiaceae, as for all other vascular cryptogams. According to HOLLE (14) a four-sided apical cell is found in the stem of the young sporophyte and is retained permanently. BOWER (2) describes for mature plants a 4 or 5-celled meristem meeting at the intersection of two more or less perpendicular lines. CAMPBELL (4) found that in some cases at least the apex of the stem is occupied by a single initial. FARMER and HILL (9) describe an apical cell of irregular prismatic form,

though sometimes triangular in cross-section, in the apex of the young stem of *Angiopteris*, and BREBNER (3) concluded that *Danaea* was the same.

Such differences of opinion show that there is either variation or vagueness in the structure observed. In this case both enter into the result. In very young stems there is a triangular pyramidal apical cell (fig. 31). This soon becomes prismatic, and the outline of the triangle in cross-section becomes irregular (fig. 32). Gradually it becomes four-sided (fig. 33). Then one of the latest segments begins to act as an apical cell, and there are two blocks of meristematic cells at the apex (fig. 34). In longitudinal view two sections separated from each other show two large vacuolate cells cutting off segments from the base. The division of the segments is very irregular. In a still larger stem the apex was occupied by a meristem (fig. 35).

The growing point of the young stem is close to the base of the youngest leaf and very narrow (fig. 36). As the stem grows older the apex grows broader. At the solenostelic stage the tissue below the center of the apical cell is large-celled pith (fig. 37).

The root apex has received more attention than that of the stem. The three-sided cell, probably derived from the octant of the embryo, has been observed in *Angiopteris*. A similar cell occurs in the apex of the very young primary root of *Marattia*. As in the stem, a four-sided prism soon appears, which HOLLE (14) thought was permanent. SCHWENDENER (25) held that it divided into four about the axis of the root, and BOWER (2) agreed with him. RUSLOW (23) found a group of initials. KOCH'S (16) explanation for the different situations that occur is ingenious. The evidence, however, of a regular sequence of divisions and fan-shaped growth of one segment with consequent shifting to the center is not entirely convincing. A possible explanation is that there is no fixed structure or behavior in the apex of the root.

New roots originate in the meristematic region of the stem before differentiation of tissue has begun. FARMER and HILL (9) maintain that the origin is a single six-sided prismatic cell of the endodermis cutting on the sides and ends. According to DE BARY (6)



root origin in pteridophytes, with the exception of Lycopodiales, is endodermal, as contrasted with the prevailing pericyclic root origin in seed plants. In *Marattia* the pericycle is not a true pericycle, since it is composed of sister cells of the endodermis, and the phloem may abut on the endodermis. Roots originate within the undifferentiated cylinder (fig. 38). Periclinal divisions work outward and laterally (fig. 39) and into the cortex which forms the periblem of the young root (figs. 40, 41).

The chief work on apical regions was done under the influence of HANSTEIN's theory of a rigid morphological distinction between periblem, plerome, and dermatogen. SCHOUTE (24) has shown that the apical divisions do not determine the limits of the tissues developed from them. This leads to the view that the character of the apical region is determined by the bulk of the organ and has no other significance. Whether the transition from the fernlike apical cell to a meristematic region has any phylogenetic significance, must be determined by finding whether other bulky plants show this variability. Some species of *Selaginella* have more than one apical cell (RUSSOW 23), but with this exception *Marattia* is unique in this character.

#### MUCILAGE DUCTS

Soon after the solenostelic stage is established, a mucilage duct may appear in the center of the pith. A branch from it runs out along the adaxial side of each leaf trace, and branches and anastomoses in the cortex of the stem and petiole. FARMER and HILL (9) follow KÜHN (19) in ascribing a lysigenous origin to these ducts. BREBNER (3) holds to the schizogenous origin in *Danaea* at the upper ends of the ducts. *Marattia* resembles *Danaea* in the division of the parenchyma cell into four to six without increase in size, and the separation of the walls where the small cells come together. The contents of the small cells stain deeply with anilin blue, and the nuclei, gathered around the point where the cells are to break apart, are small and denser than the nuclei in the surrounding parenchyma cells. The space left when the walls break apart appears empty at first, then becomes filled with a vacuolate substance that stains with anilin blue. Later the reaction of this

mucilage to stain changes rapidly and it takes the safranin. At this time and earlier than in *Danaea* the small cells begin to break down and the mucilage becomes stringy (fig. 41). The small cells do not break down uniformly; they may extend into the cavity of the duct as the "bridge-cells" of *Danaea* or float in the mucilage. The schizogenous stage may be omitted and cells of the pith break down into mucilage directly. Although tannin cells are numerous, none appeared to be changing to mucilage ducts as LUTZ (20) describes for *Angiopteris*. The origin and development of the mucilage ducts in the seedling of *Microcycas* are identical with those of *M. alata*.

### Summary and conclusions

1. The transition from protostele to solenostele in *Marattia* is sudden and without the intervention of a definite medullated monostelic stage. The indefinite hints of pith due to the early start of parenchyma to divide leaf trace from stele may be the origin of the medullated stage.

2. The medullary system of *Marattia* differs from that of the solenostelic ferns in origin, course of bundles, and development into a cylinder. It resembles that of *Psaronius* in its relation to leaf traces.

3. Elongation of the stem causes the union of the bundles into broad bands and a reduction of the medullary system. This emphasizes the close relation between the compact habit and crowded leaves of *Marattia* and the number of concentric cycles and leaf gaps in the dictyostele. The difference in habit, therefore, accounts for the difference in the anatomy of *Marattia* and the more elongated Marattiaceae, *Danaea*, and *Kaulfussia*, and the treelike *Psaronius*.

4. The occurrence and position of protoxylem varies. It may not be distinguishable or may consist of spiral or modified reticulate tracheids. When distinguishable, it may be in an exarch or mesarch position in the cotyledonary node, mesarch in the protostele above the cotyledonary node, and usually endarch in the strands of the older parts of the stem. Similar variations occur in the leaf traces. The cotyledonary trace may change from

exarch to mesarch, the later leaves from mesarch to endarch. Mature leaf traces are endarch.

5. Apical meristems vary from the fernlike triangular apical cells in young sporelings to meristematic groups in older stems and roots. Such variation during the course of development occurs in the gametophytes of pteridophytes and in some liverworts, but is not recorded for the sporophyte of other ferns.

6. The cotyledonary trace is collateral during most of its course. Later leaf traces start collateral and develop adaxial sieve tubes in their course through the cortex. Some stems show a slight tendency toward a reduction of internal phloem and endodermis, others an increase in the older part of the stem. The basis for classifying the Marattiaceae with pteridophytes that have developed collateral bundles is therefore insecure.

7. Secondary roots originate from vascular tissue before differentiation into regions has begun. The cortex shares in forming the cortex of the root.

8. Mucilage ducts originate both schizogenously and lysigenously, generally the former.

Marked instability is characteristic of *Marattia*. The Ophioglossaceae share this trait in root structure, the Dicksonieae in protoxylem position. Only gametophytes have such a transition of apical regions. Combined with variability is the indefiniteness of the medullated monostelic stage. Such instability is characteristic of plants that give rise to new lines. It is evident that the Marattiaceae have retained many characters of the stock from which branched off the Ophioglossaceae, then the Psaronieae and Cyatheaceae. It is probable that the compact habit of the Marattiaceae was developed after the lines connecting with the other families had diverged, since the characteristics due to it are also unstable.

This investigation was carried on at the University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. W. J. G. LAND, to whom I wish to express my thanks for criticism and advice.

## LITERATURE CITED

1. BOODLE, L. A., On the anatomy of the Schizeaceae. *Annals of Botany* **15**:359-421. *pls.* 19-21. 1901.
2. BOWER, F. O., The origin of a land flora. London. 1908.
3. BREBNER, G., On the anatomy of *Danaea* and other Marattiaceae. *Annals of Botany* **16**:517-552. *pls.* 22, 23. 1902.
4. CAMPBELL, D. H., Mosses and ferns. London. 1905.
5. CHRYSLER, M. A., The nature of the fertile spike in Ophioglossaceae. *Annals of Botany* **24**:1-18. *figs.* 1-16. *pls.* 1, 2. 1910.
6. DE BARY, A., Comparative anatomy of phanerogams and ferns. English translation. Oxford. 1884.
7. DE VRIES, W. H., and HARTING, P., Monographie des Marattiacées. 1853.
8. DORETY, HELEN A., The seedling of *Ceratozamia*. *BOT. GAZETTE* **46**: 205-220. *pls.* 12-16. 1908.
9. FARMER, J. B., and HILL, T. G., On the arrangement and structure of the vascular strands in *Angiopteris evecta* and some other Marattiaceae. *Annals of Botany* **16**:371-402. *pls.* 16-18. 1902.
10. GWYNNE-VAUGHAN, D. T., Observations on the anatomy of the solenostelic ferns. I. *Loxsonia*. *Annals of Botany* **15**:71-98. *pl.* 3. 1901.
11. ———, Observations on the anatomy of the solenostelic ferns. II. *Annals of Botany* **17**:689-742. *pls.* 33-35. 1903.
12. ———, On the anatomy of *Archangiopteris Henryi* and other Marattiaceae. *Annals of Botany* **19**:259-271. *pl.* 10. 1905.
13. HOFMEISTER, W., Beiträge zur Kenntniss der Gefässkryptogamen. II. *Abh. Kgl. Gesell. Wiss. Leipzig* **3**:603-682. *pls.* 1-13. 1857.
14. HOLLE, H. G., Ueber die Vegetationsorgane der Marattiaceae. *Nach. Kgl. Gesell. Wiss. Göttingen* 1876:16-24; *Bot. Zeit.* **34**:215-220. 1876.
15. JEFFREY, E. C., The structure and development of the stem in pteridophytes and gymnosperms. *Phil. Trans. Roy. Soc. B* **195**:119-146. *pls.* 1-6. 1903.
16. KOCH, L., Ueber Bau und Wachstum der Wurzelspilze von *Angiopteris evecta*. *Jahrb. Wiss. Bot.* **27**:369-402. *pls.* 15, 16. 1895.
17. KÜHN, R., Untersuchungen über die Anatomie der Marattiaceen und anderer Gefässkryptogamen. *Flora* **72**:457-521. *pls.* 18-20. 1889.
18. LANG, W. H., On the prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica*. *Annals of Botany* **16**:23-56. *pls.* 1-3. 1902.
19. LECLERC DU SABLON, Recherches sur la formation de la tige des fougères. *Ann. Sci. Nat. Bot.* VII. **11**:1-16. *pls.* 1, 2. 1890.
20. LUTZ, M. L., Sur l'origine des canaux gommifères des Marattiacées. *Jour. Botanique* **12**:133-135. *pl.* 2. 1898.
21. METTENIUS, G., Ueber den Bau von *Angiopteris*. *Abh. Kgl. Sachs. Gesell. Wiss.* **6**:501-570. *pls.* 1-10. 1864.

22. RUDOLPH, K., Psaronien und Marattiaceen, vergleichende anatomische Untersuchung. Sitz. Kgl. Akad. Wiss. Wien **78**:165-201. *pls. 1-3*. 1905.
23. RUSSOW, E., Vergl. Untersuchungen der Leitbündel der Kryptogamen. Mém. Akad. Imp. Sci. St. Pétersbourg VII **19**:x+207. *pls. 1-11*. 1872.
24. SCHOUTE, J. C., Die Stelar-Theorie. Groningen. 1902.
25. SCHWENDENER, S., Ueber Scheitelwachstum der Phanerogamen Wurzeln. Sitz. Kgl. Akad. Wiss. Berlin **1**:183-199. *pls. 6, 7*. 1882.
26. SHOVE, MISS R. F., On the structure of the stem of *Angioperis evecta*. Annals of Botany **14**:497-525. *pls. 28, 29*. 1900.
27. TANSLEY, A. G., and LULHAM, MISS R. B. J., On a new type of fern stele and its probable phylogenetic relations. Annals of Botany **16**:157-164. *figs. 1-18*. 1902.
28. ———, A study of the vascular system of *Matonia pectinata*. Annals of Botany **19**:475-519. *pls. 32, 33*. 1905.

### EXPLANATION OF PLATES IX-XII

With the exception of figs. 4, 5, 11-21, and 25, all drawings were made with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are as follows: *c*, cotyledon; *en*, endodermis; *l*, leaf; *lb*, leaf base; *lt*, leaf trace; *ms*, medullary strand; *pa*, parenchyma; *ph*, phloem; *pph*, protophloem; *pr*, prothallium; *px*, protoxylem; *r*, root; *rt*, root trace; *s*, sieve tube; *st*, stipule; *x*, xylem.

FIG. 4.—Young sporeling attached to the prothallium, with the second leaf appearing.  $\times 2.5$ .

FIG. 5.—Older sporeling, showing persistent leaf bases (*lb*).  $\times 1$ .

FIG. 6.—Transverse section through the cotyledonary node, showing parenchyma cells among the xylem.  $\times 400$ .

FIG. 7.—Transverse section through the stele, showing apparent pith due to the simultaneous departure of the root trace (*rt*) and leaf trace (*lt*) opposite each other.  $\times 188$ .

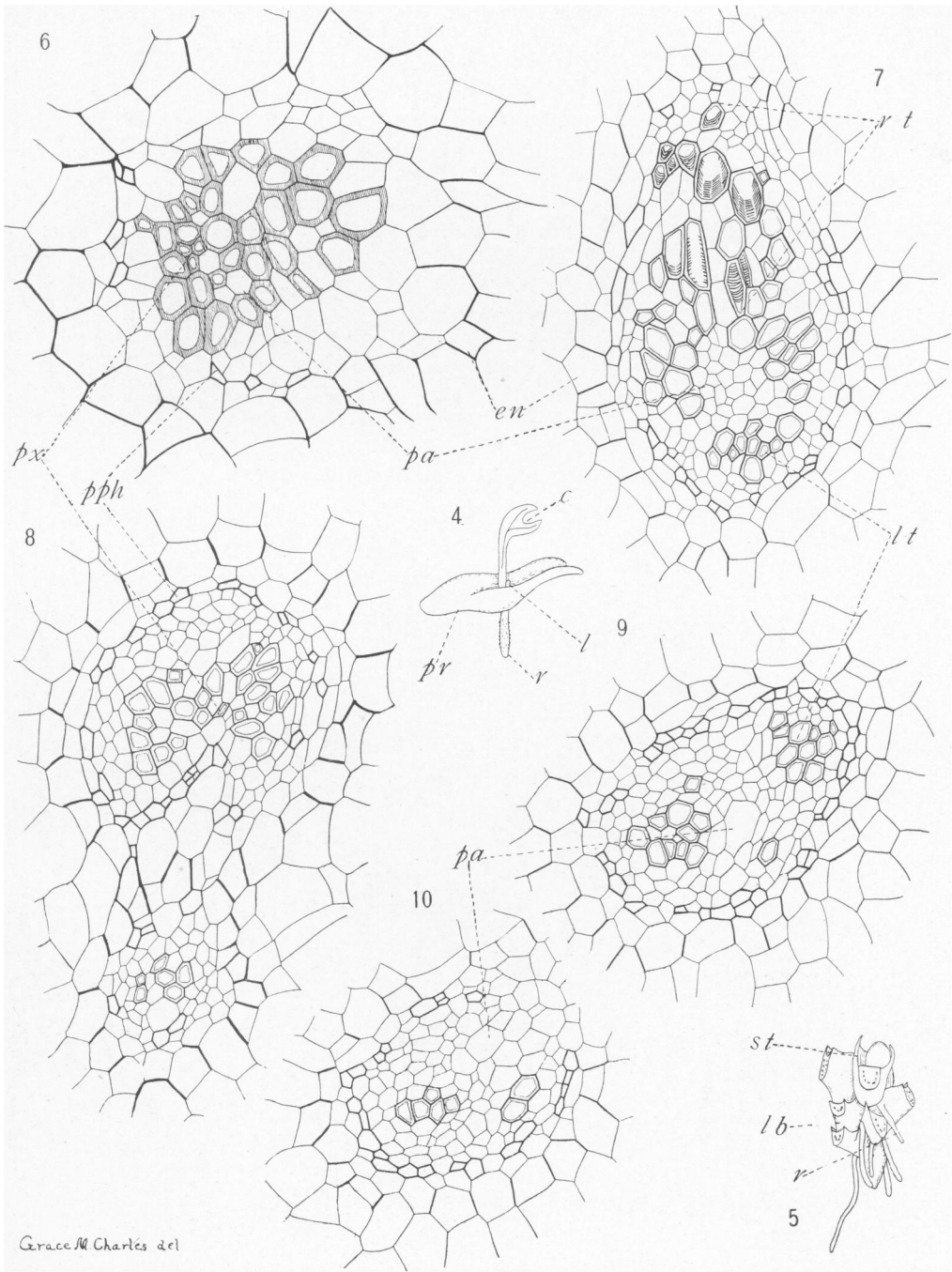
FIG. 8.—Transverse section of the same  $50\mu$  above fig. 7, showing phloem (*ph*) and endodermis (*en*) cutting in a curve behind a leaf trace.  $\times 188$ .

FIG. 9.—Transverse section of the same  $40\mu$  above fig. 8, showing the departure of the next leaf trace (*lt*) and a persistent cell of cortical parenchyma (*pa*).  $\times 188$ .

FIG. 10.—Transverse section of the same  $40\mu$  above fig. 9, showing cortical parenchyma (*pa*) at the side of the stele, contrasting with xylem parenchyma in size.  $\times 188$ .

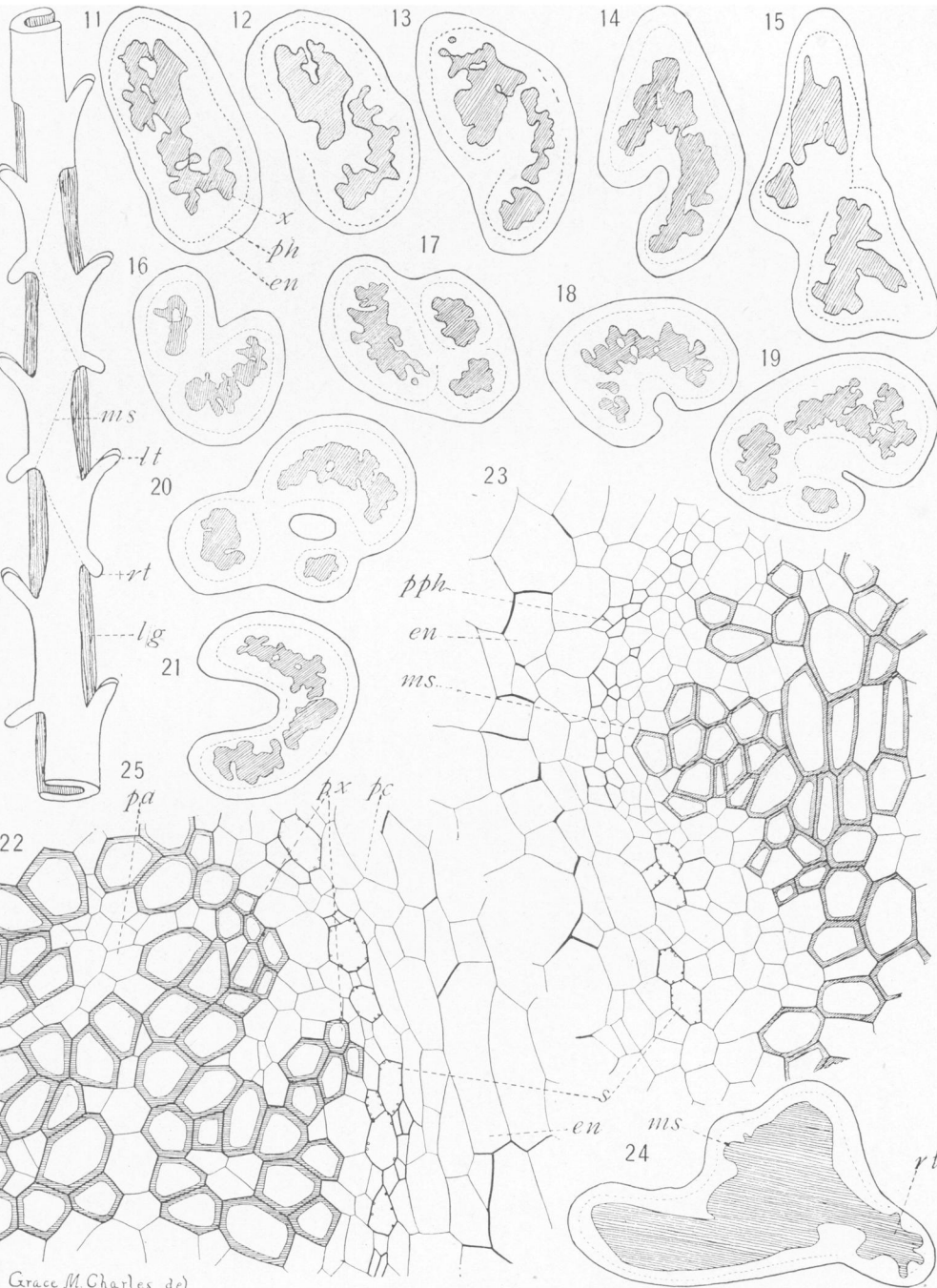
FIGS. 11-21.—Diagrams of successive stages in the transition from protostele to solenostele.

FIG. 22.—Transverse section from the inner surface of a dictyostelic bundle, showing endarch protoxylem, bands of parenchyma, sieve tubes, pericycle, and endodermis.  $\times 188$ .

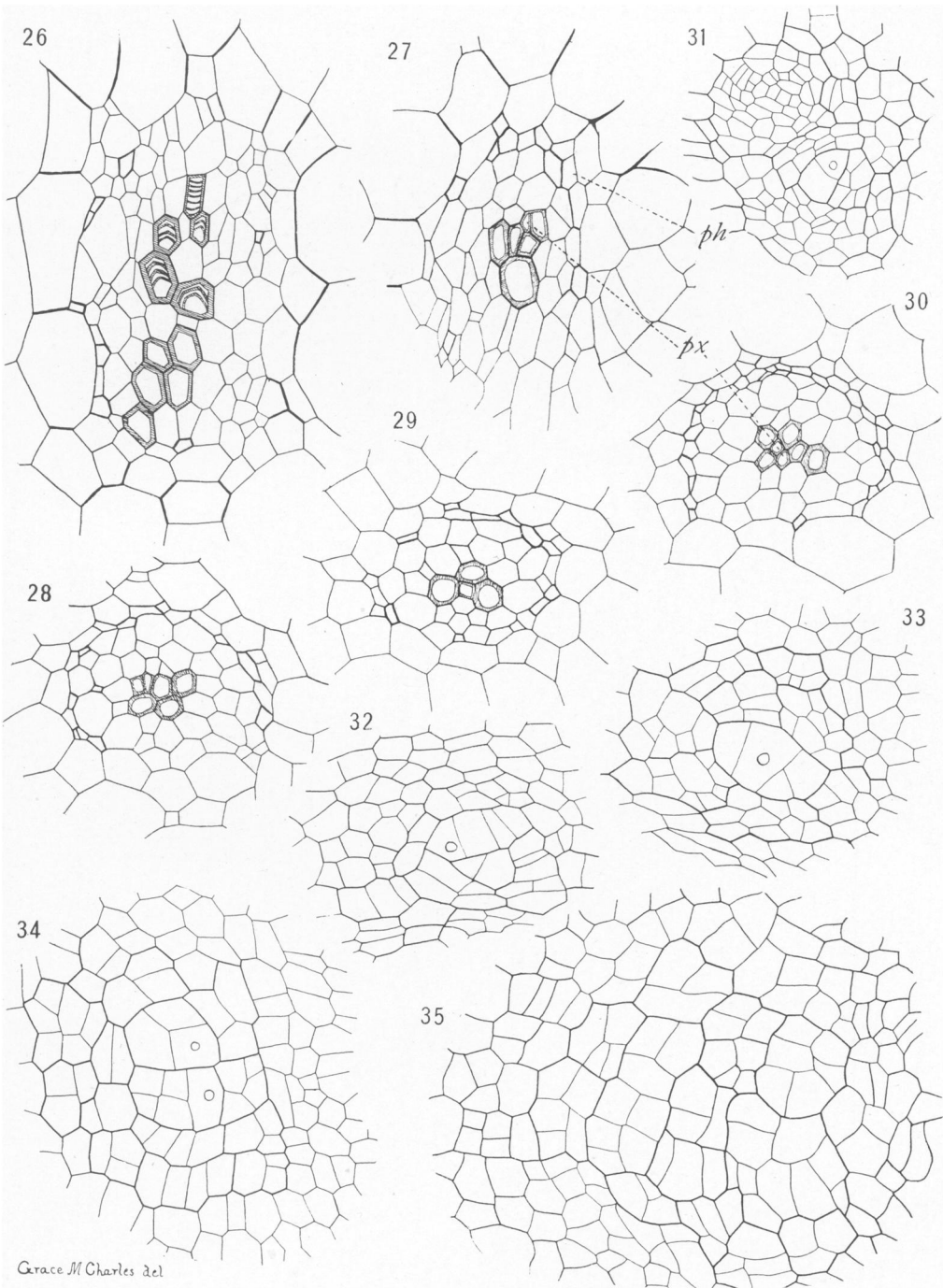


Grace M. Charles del

CHARLES on MARATTIA

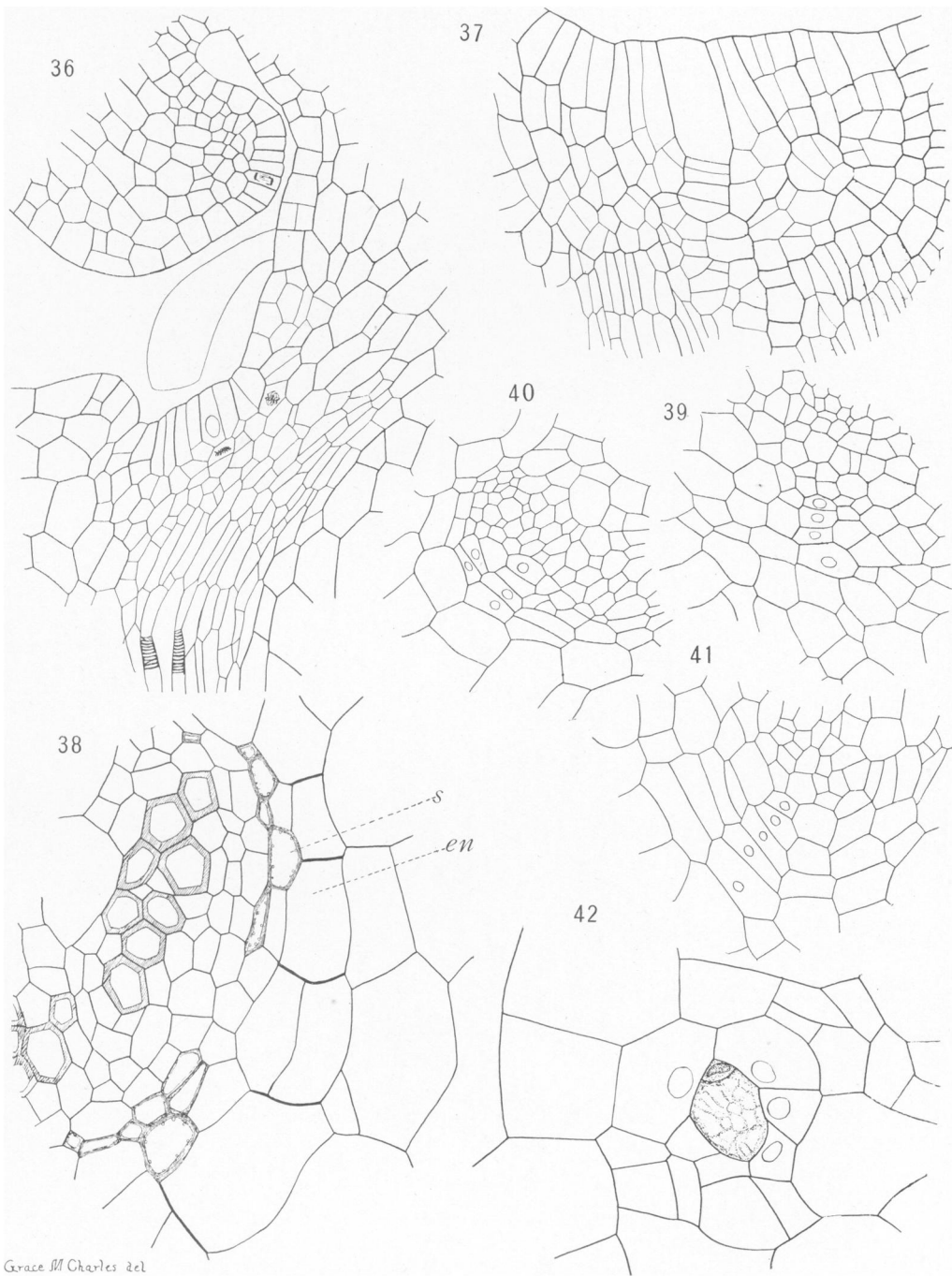


CHARLES on MARATTIA



CHARLES on MARATTIA





Grace M Charles del

CHARLES on MARATTIA

FIG. 23.—Origin of the medullary strand from the inner surface of a strand of the dictyostele.  $\times 188$ .

FIG. 24.—Diagram of the strand of the dictyostele at fig. 23, showing the relation of the origins of medullary strand and root trace.

FIG. 25.—Diagram of the vascular cylinder, showing the relation of the medullary strand to leaf gaps and leaf traces.

FIG. 26.—Transverse section of the cotyledonary node, showing the departure of an exarch leaf trace.  $\times 400$ .

FIGS. 27-30.—Transverse sections of the cotyledonary trace, showing the transition from exarch to mesarch protoxylem.  $\times 400$ .

FIG. 31.—Transverse section of the apical region of a sporeling with six leaves, showing the triangular apical cell and large segment; at the left above is the youngest leaf trace.  $\times 188$ .

FIG. 32.—Transverse section of apical region of a sporeling with 25 leaves, showing an irregular apical cell.  $\times 188$ .

FIG. 33.—Transverse section of an older stem, showing a four-sided apical cell.  $\times 188$ .

FIG. 34.—Transverse section of a stem 6 mm. in diameter, showing two meristematic blocks of cells.  $\times 188$ .

FIG. 35.—Transverse section of the apex of a stem 12 mm. in diameter, showing a meristematic region.  $\times 188$ .

FIG. 36.—Longitudinal section of the apical region of a very young sporeling.  $\times 400$ .

FIG. 37.—Longitudinal section of the apical region of a stem with 30 leaves; the tissue below the apical cell is pith; at the sides is vascular meristem.  $\times 188$ .

FIG. 38.—Transverse section of a young stele, showing a frequent relation of sieve tubes to endodermis.  $\times 400$ .

FIG. 39.—Transverse section near the apex, showing early origin of root from vascular meristem.  $\times 130$ .

FIGS. 40, 41.—Transverse sections of later stages in the development of roots than fig. 39.  $\times 130$ .

FIG. 42.—Transverse section of a mucilage duct, showing a cell disintegrating in the mucilage.  $\times 400$ .